

Research Article

Campanophyllum microsporum (Agaricales, Agaricomycetes), Calocera multiramosa, and Dacrymyces naematelioides (Dacrymycetales, Dacrymycetes), three new species from Yunnan Province, southwestern China

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Abstract

Three new species belonging to Basidiomycota from southwestern China are described based on morphological and molecular data. Campanophyllum microsporum is morphologically characterized by dorsally pseudostipitate, pale orange to brownish orange pileus, excentric to lateral pseudostipe, crowded lamellae, cylindrical-ellipsoid basidiospores $3.0-4.2 \times 1.7-2.2 \mu m$, narrowly clavate to clavate basidia $14.5-23.0 \times 3.0-4.2 \mu m$, and cylindrical to clavate cheilocystidia 22.0-55.0 × 5.0-10.8 µm. Calocera multiramosa is morphologically characterized by stipitate, yellowish to orange, dendroid, and dichotomously branched basidiomata, cylindrical to clavate basidia 36.5-52.5 × 3.8-6.1 μm, navicular or reniform, 1-5-septate mature basidiospores $10.4-16.7 \times 5.2-7.4 \mu m$. Dacrymyces naematelioides is morphologically characterized by stipitate and cerebriform, orange to light brown basidiomata, cylindrical to clavate, smooth or roughened basidia $38.5-79.5 \times 6.5-10.6 \mu m$, broadly and elliptic-fusiform, 7-septate mature basidiospores $18.5-28.6 \times 8.9-13.8 \mu m$. These three new species are supported by the phylogenetic analyses using maximum likelihood (ML) and Bayesian inference (BI) analyses with combined nuclear ribosomal DNA (rDNA) internal transcribed spacer (ITS) and large ribosomal subunit (LSU) sequences. Full descriptions and photographs of these new species are provided.

Key words: Basidiomycota, new taxon, phylogenetic analyses, taxonomy

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Introduction

The monotypic genus *Campanophyllum* Cifuentes & R.H. Petersen was proposed to accommodate *Lentinus proboscideus* Fr., traditionally contains dorsally pseudostipitate pileus with tricholomataceus, excentric to lateral pseudostipe, crowded lamellae, cylindrical-ellipsoid spores, cylindrical, clavate to utriform cheilocystidia, and grows on rotten wood (Cifuentes et al. 2003). *L. proboscideus* was combined into the genus *Campanophyllum* in the family Cyphellaceae, and

designated a neotype by Cifuentes et al. (2003). In addition, the authors demonstrated that this species represents a novel species of a novel genus distinct from its closest relatives through a comprehensive analysis of morphological characteristics, molecular data, and sexual compatibility (Cifuentes et al. 2003). The species was found in montane forests in Colombia, Costa Rica, Ecuador, Mexico, and Panama, and is currently being assessed for inclusion in the IUCN red list as endangered (https://redlist.info/iucn/species_view/488791/) (Cifuentes et al. 2003; Reschke et al. 2021). Recently, researchers also collected the species of *C. proboscideum* in India and studied its fungal extracts, which are rich in natural antioxidants and highly effective antimicrobial activity (Borthakur et al. 2020). However, the specimens collected from India may not be of *C. proboscideum*, but of another species, due to the huge differences in the ITS sequences. The absence of detailed morphological descriptions precludes the ability to ascertain the specific species to which the specimen belongs.

Calocera (Fr.) Fr. and Dacrymyces Nees are the two major polyphyletic groups in the family Dacrymycetaceae, characterized by pulvinate to dendroid or cerebriform basidiomata (Shirouzu et al. 2007, 2009, 2013, 2017; Zamora and Ekman 2020; Fan et al. 2021; Lian et al 2022; Zamora et al. 2022). Their classifications in Dacrymycetes are based on morphology and have remained unaltered (McNabb 1965, 1973; Shirouzu et al. 2017; Zamora and Ekman 2020). However, this morphology-based classification has often conflicted with the results of molecular phylogenetic analyses, and Calocera, Dacrymyces, and Dacryopinax G.W. Martin have been shown to be non-monophyletic genera (Shirouzu et al. 2013, 2017; Zamora and Ekman 2020). Phylogenetic analysis shows that species of Calocera and Dacrymyces are distributed in many clades of the family Dacrymycetaceae. The three species of *C. cornea* (Batsch) Fr., *C. lutea* (Massee) McNabb, and C. fusca Lloyd were clustered into three distinct clades, rather than forming a single clade, despite belonging to the same genus, and many of the species of *Dacrymyces* were grouped with other genera in one clade (Shirouzu et al. 2017; Zamora and Ekman 2020).

Calocera is ecologically saprobic, causing brown rot except *C. viscosa* (Pers.) Bory, and *C. lutea* which are white rot species (Shirouzu et al. 2009, 2013). According to the Index Fungorum (https://www.indexfungorum.org) as of June 2024, 95 species names of *Calocera* are recorded. In China, only six species have been reported: *C. sinensis* McNabb, *C. hunanensis* B. Liu & K. Tao, *C. mangshanensis* B. Liu & L. Fan, *C. morchelloides* B. Liu & L. Fan, *C. bambusicola* Sheng H. Wu, and *C. tibetica* F. Wu, L.F. Fan & Y.C. Dai (McNabb 1965; Liu et al. 1988; Liu and Fan 1989, 1990; Fan et al. 2021). *Dacrymyces* described by Nees (1816) based on *D. stillatus*, is treated as a genus of saprotrophic fungi (Shirouzu et al. 2009; Zamora and Ekman 2020; Zamora et al. 2022). A total of 234 species names of *Dacrymyces* is recorded in the Index Fungorum in June 2024, and the genus appears to be the most polyphyletic in the phylogeny of the Dacrymycetales (Shirouzu et al. 2017; Zamora and Ekman 2020; Savchenko et al. 2021; Zamora et al. 2022).

The Laojun Mountain is one of the main parts of the Three Parallel Rivers of Yunnan Protected Areas (TPRYPA), the World Natural Heritage Site, in northwest Yunnan Province, southwestern China. The TPRYPA is part of the Mountains of Southwest China Biodiversity Hotspot, which includes 12,000 plant species, 29 percent of which are found nowhere else (Zhang et al. 2010; Mittermeier et al. 2011).

The Laojun Mountain is located between 26°2.80′–27°36.60′N, 99°1.20′–99°54.60′E and includes four counties, including Yulong, Jianchuan, Lanping, and Weixi, with an area of about 108,500 hm² and elevations ranging from 2,100 to 4,513 m (Zhang et al. 2010). The dominant tree species in Laojun Mountain are *Abies* sp., *Acer* sp., *Betula* sp., *Cyclobalanopsis* sp., *Fargesia* sp., *Lithocarpus* sp., *Picea* sp., *Pinus* sp., *Quercus* sp., *Rhododendron* sp., and *Sorbus* sp. (Wu and Zhu 1987).

During the investigation of the diversity of macrofungi in the Laojun Mountain, a multitude of specimens, including a dozen belonging to the *Campanophyllum* genus and several belonging to the genera *Calocera* and *Dacrymyces*, were collected from July to September 2019–2023. In this study, the specimens of these three new species were collected from the same position in a deciduous forest of the Laojun Mountain. With the combination of morphological observations and phylogenetic analyses, we described three new species, namely *Campanophyllum microsporum*, *Calocera multiramosa*, and *Dacrymyces naematelioides*.

Materials and methods

Specimen collection, morphological observation, and isolation

The fungal specimens used in this study were collected from the Laojun Mountain in northwestern Yunnan Province, China. After collection, the specimens were dried in an electric drier at ca. 45 °C, and deposited in the Herbarium of Cryptogams, Kunming Institute of Botany of the Chinese Academy of Sciences (HKAS). Macromorphological characteristics and habitats were obtained from field notes and photographs. Color codes were based on Kornerup and Wanscher (1978). Micromorphological features were observed from the dried specimens and measured and photographed in 5% KOH solution (w/v) and 1% Congo Red solution (w/v) using a Leica DM6 B upright light microscope and Leica Application Suite X (LAS X, version 3.7.5). In the description of basidiospores, the abbreviations m/n/p denote m basidiospores measured from n basidiomata of p collections. The dimensions of the microscopic structures are given as (a–) b–c (–d), in which b–c contains at least 90% of the measured values, and (a-) and (-d) are the extreme values provided in parentheses. The Q value stands for the ratio of length/width of an individual basidiospore and basidium, and L_m/W_m/Q_m refers to the average length/width/Q value of all basidiospores (Na et al. 2022; Wei et al. 2024). The strains of Campanophyllum microsporum were isolated from the inner tissue of fresh basidiomata using a Yeast Extract Peptone Dextrose Agar (YPD) Medium consisting of 2 g yeast extract (Beijing Aoboxing Biotech Co., Ltd.), 2 g peptone (Beijing Aoboxing Biotech Co., Ltd.), 20 g dextrose (Tianjin Fengchuan Chemical Reagent Co., Ltd.), 13 g agar (Biosharp Life Sciences), and 1000 mL distilled water. The living cultures were preserved at the National Germplasm Bank of Edible Mushroom (Yunnan). Their isolate IDs are YAASM 7490 and 7491.

DNA extraction, PCR amplification and sequencing

The genomic DNA was extracted from the dry specimens and cultured mycelia using the Fungal gDNA kit GD2416 (Biomiga CA, USA) following the manufacturer's instructions. The entire ITS and partial LSU of the nrDNA region were

amplified from the total DNA using the primer pair ITS5/ITS4 (White et al. 1990) and LR0R/LR7 (Vilgalys and Hester 1990; Moncalvo et al. 2000), respectively, and no DNA template was used as the negative control. The PCR cycling for the amplification of both ITS and LSU was as set follows: an initial denaturation at 95 °C for 3 min, followed by 34 cycles of 95 °C for 30 s, 56 °C for 1 min, 72 °C for 1 min, and a final extension at 72 °C for 5 min. The PCR products were sequenced bi-directionally by Tsingke Biotechnology Co., Ltd. Kunming, China. Newly generated sequences of both directions were assembled using the software SeqMan version 11.1.0 (DNASTAR, Inc.), and submitted to GenBank (accession nos. ITS: PP550870–PP550882, LSU: PP550017–PP550027).

Sequence alignment and phylogenetic analyses

The sequences used in this study were those retrieved from GenBank combined with newly generated sequences. Taxon information and GenBank accession numbers of all the sequences are listed in Table 1. All sequences were aligned using the software MAFFT 7.503 (Katoh and Standley 2013) with the default settings and edited manually using BioEdit 7.2.5 (Hall 1999). After alignment, the ITS and LSU datasets were concatenated using the program SequenceMatrix 1.8.1 (Vaidya et al. 2011). Phylogenetic analyses of Cyphellaceae and Dacrymycetaceae were performed using maximum likelihood (ML) and Bayesian inference (BI) analyses based on the sequences matrix on the personal computer. The best-fit models for the concatenated ITS+LSU dataset were selected according to the Akaike Information Criterion (AIC) in jModelTest 2.1.10 (Guindon and Gascuel 2003; Darriba et al. 2012). ML analyses of the concatenated ITS+LSU dataset of Cyphellaceae and Dacrymycetaceae were performed using RAxML-NG 1.1.0 (Kozlov et al. 2019) under the GTR+I+G model with 1,000 bootstrap replicates. BI analyses of Cyphellaceae and Dacrymycetaceae were implemented using MrBayes 3.2.7 (Ronquist et al. 2012) under the GTR+I+G model. There were four independent runs, each of which had four chains for 15,000,000 generations sampling from the posterior distribution every 1000th generation. The first 25% of the sampled trees were discarded as burn-in, while the remaining trees were used to obtain the Bayesian posterior probabilities of the clades. The constructed phylogenetic trees were visualized and edited in FigTree 1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/) and Adobe Illustrator 25.3.1. Flammulina velutipes (Curtis) Singer, was used as an outgroup in the phylogeny of Cyphellaceae (Vizzini et al. 2022), while Suillus pictus (Peck) Kuntze, and Coprinus comatus (O.F. Müll.) Pers., were used as the outgroup in the phylogeny of Dacrymycetaceae (Shirouzu et al. 2013). The final alignments and the retrieved topologies were deposited in TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S31416) with submission ID 31416.

Results

Phylogenetic analyses

In the phylogeny of Cyphellaceae, 36 sequences were used for phylogenetic analyses, of which four sequences were newly generated in this study. The concatenated dataset of ITS and LSU sequences comprised a total of 1695 characters.

Table 1. Taxa used in the phylogenetic analyses and their corresponding GenBank accession numbers. Newly generated sequences are in bold. Type materials are marked with 'T'.

Species	Isolate ID /Voucher	Country	Gendank Acce	ssion Numbers	Reference
			ITS	LSU	
Agaricomycetes					
Campanophyllum microsporum	- /HKAS 133167	China	PP550870	PP550018	this study
C. microsporum	- /HKAS 133168	China	PP550871	PP550019	this study
C. microsporum	- /HKAS 133169	China	PP550872	PP550020	this study
C. microsporum	- /HKAS 133170 [™]	China	PP550873	PP550017	this study
C. proboscideum	- /TENN56402	Mexico	AY230866	AY230866	Cifuentes et al. (2003)
C. proboscideum	- /TENN56427	Mexico	AY230867	AY230867	Cifuentes et al. (2003)
C. proboscideum	- /PA46	Panama	MW386067	-	Reschke et al. (2021)
C. proboscideum	- /PAN327	Panama	MW386071	-	Reschke et al. (2021)
C. proboscideum	- /PAN373	Panama	MW386072	-	Reschke et al. (2021)
C. proboscideum	- /NEHU.MBSRJ. 38	India	KP843881	-	unpublished
Chondrostereum coprosmae	- /PDD: 119544	New Zealand	OL709440	_	unpublished
C. coprosmae	- /PDD: 89940	New Zealand	OL709437	OL709436	unpublished
C. purpureum	HHB-13334-sp. /-	USA	AF518607	- 1	Hibbett and Binder (2002)
C. purpureum	SFI-B18 /-	Ireland	MT535785	MT559785	unpublished
C. purpureum	14-2300 /-	USA	MG774405	-	Merlet et al. (2018)
C. purpureum	CBS 350.53 /-	France	MH857241	MH868775	Vu et al. (2019)
C. vesiculosum	- /PDD: 119640	New Zealand	OR607672	-	unpublished
Cunninghammyces umbonatus	– /He 5316	China	MW557955	-	unpublished
C. umbonatus	– /He 5311	China	MW557940	MW557954	unpublished
C. umbonatus	– /He 5313	China	MW557941	-	unpublished
Cyphella digitalis	- /PVKU3421	Czech Republic	OM837174	-	Holec et al. (2022)
C. digitalis	Thorn-617 /-	USA	AY293175	-	Binder et al. (2005)
C. digitalis	CBS 679.82 /-	USA	DQ486698	AY635771	Matheny et al. (2006)
Gloeostereum incarnatum	G1905 /HCC-3	Russia	MK278092	-	Varga et al. (2019)
G. incarnatum	- /KUC20131022-28	South Korea	KJ668540	KJ668393	Jang et al. (2015)
G. incarnatum	3332 /-	Sweden	AF141637	- 1	Parmasto and Hallenberg (2000
G. incarnatum	- /NIFoS 1948	South Korea	MH992519	- 1	unpublished
G. incarnatum	BCC 41461 /-	Thailand	KY614001	KY614002	unpublished
G. cimri	CBS 145006 ^T /-	Netherlands	MT023735	MN266884	Ahmed et al. (2020)
Granulobasidium vellereum	G0482 /DK 2781	Poland	MK278094	_	Varga et al. (2019)
G. vellereum	CBS 52.84 /-	USA	AY745729	-	unpublished
G. vellereum	– /B. Gilsenius (GB)	Sweden	DQ677490	_	Larsson (2007)
G. vellereum	BAFCcult 4367 /-	Argentina	KC881193	_	Robles et al. (2015)
G. vellereum	TJU_NOV19 /-	China	OM237077	-	unpublished
Incrustocalyptella columbiana	- /K:237992	United Kingdom	MW830122	_	unpublished
Flammulina velutipes	AFTOL-ID 558 /-	USA	AY854073	AY639883	unpublished
Dacrymycetes		1	l .		·
Calocera cornea	CBS 124.84 /-	Canada	AB712437	AB472738	Shirouzu et al. (2013)
C. cornea	ICMP 20465 /PDD 104991	New Zealand	LC131403	LC131362	Shirouzu et al. (2017)
C. cornea	AFTOL-ID 438 /-	unknown	AY789083	AY701526	unpublished
				LC131363	<u> </u>
C. cornea	ICMP 21223 /PDD 107847	New Zealand	LC131404		Shirouzu et al. (2017)
C. cornea	- /UPS F-940774	Sweden	MN595626	MN595626	Zamora and Ekman (2020)
C. cornea	- /CWU(MYC)6922	Ukraine	MW191969	MW159089	Savchenko et al. (2021)
C. furcata	– /H:Spirin 10949	Russia	MW191975	MW159088	Savchenko et al. (2021)

Species	Isolate ID /Voucher	Country	GenBank Accession Numbers		Reference
			ITS	LSU	
C. furcata	- /TU135016	Estonia	MW191958	MW159087	Savchenko et al. (2021)
C. tibetica	- /Dai20171 [⊤]	China	MW549777	MW750403	Fan et al. (2021)
C. tibetica	- /Dai20178	China	MW549778	MW750404	Fan et al. (2021)
C. multiramosa	− /HKAS 133171 [™]	China	PP550874	PP550021	this study
C. multiramosa	- /HKAS 133172	China	PP550875	PP550022	this study
C. multiramosa	- /HKAS 133173	China	PP550876	PP550023	this study
C. viscosa	AFTOL-ID 1679 /MW 591	Germany	DQ520102	DQ520102	unpublished
C. viscosa	TUFC12873 /TNS-F-15704	Japan	AB712439	AB299048	Shirouzu et al. (2013)
C. viscosa	- /UPS F-940773	Sweden	MN595628	MN595628	Zamora and Ekman (2020)
C. viscosa	- /CWU(MYC)6937	Ukraine	MW191970	MW159090	Savchenko et al. (2021)
Cerinomyces aculeatus	− /TUMH61942 (TUFC50098) ^T	Japan	MW191955	MW159053	Savchenko et al. (2021)
C. atrans	TUFC 30545 /-	Canada	AB712443	AB712423	Shirouzu et al. (2013)
C. borealis	− /O160848 [™]	Norway	MW191890	MW159042	Savchenko et al. (2021)
C. brevisetus	− /URM:Chikowski 1544 [⊤]	Brazil	MW191886	MW159046	Savchenko et al. (2021)
C. creber	− /UPS:F-946512 [†]	Spain	MW191985	MW191985	Savchenko et al. (2021)
C. enatus	TUFC12876 /TNS-F-21034	Japan	AB712441	AB472696	Shirouzu et al. (2013)
C. ramosissimus	CFMR:FP-150848 ^T /-	Belize	AB712446	AB712426	Shirouzu et al. (2013)
Dacrymyces burdsallii	CFMR:HHB-6908 ⁺ /-	USA	AB712444	AB712424	Shirouzu et al. (2013)
D. capitatus	- /Dai 20023	China	OL587808	OL546776	unpublished
•	CBS 293.82 /-		AB712450	AB472741	·
D. capitatus		Canada			Shirouzu et al. (2013)
D. ceraceus	CFMR:HHB-8969 ^T /-	USA	AB712442	AB712422	Shirouzu et al. (2013)
D. chrysocomus	- /UPS:F-940136	Spain	MN595629	MN595629	Zamora and Ekman (2020)
D. chrysocomus	- /UPS:F-940134	Sweden	MN595630	MN595630	Zamora and Ekman (2020)
). chrysospermus	TUFC13115 /TNS-F-15712	Japan	AB712452	AB299073	Shirouzu et al. (2013)
). chrysospermus	– /H:Spirin 10795	Russia	MW191974	MW159078	Savchenko et al. (2021)
D. chrysospermus	- /H:Miettinen 14818	USA	MW191961	MW159077	Savchenko et al. (2021)
). aff. Chrysospermus	- /UPS:F-593536	Japan	MN595631	MN595631	Zamora and Ekman (2020)
D. dictyosporus	CFMR:HHB-8618 /-	USA	AB712454	AB712429	Shirouzu et al. (2013)
D. estonicus	- /UPS:F-940137	Sweden	MN595632	MN595632	Zamora and Ekman (2020)
D. estonicus	- /UPS:F-940138	Sweden	MN595633	MN595633	Zamora and Ekman (2020)
D. fennicus	- /H:Miettinen 21174	Finland	MW191957	MW159071	Savchenko et al. (2021)
D. fennicus	- /UPS:F-946596	Sweden	MZ147627	MZ147627	Savchenko et al. (2021)
D. grandinioides	- /H7008841	Kenya	MW191950	MW159076	Savchenko et al. (2021)
D. lacrymalis	TUFC13327 /TNS-F-15719	Japan	AB712456	AB299069	Shirouzu et al. (2013)
D. cf. minor	- /H:Miettinen 19137	Finland	MW191967	MW159080	Savchenko et al. (2021)
D. cf. minor	- /H:Miettinen 20591	Finland	MW191965	MW159079	Savchenko et al. (2021)
D. naematelioides	- /HKAS 133174a [™]	China	PP550877	PP550024	this study
D. naematelioides	- /HKAS 133174b [™]	China	PP550878	PP550025	this study
D. naematelioides	- /HKAS 133174c [™]	China	PP550879	PP550026	this study
D. naematelioides	− /HKAS 133174d [™]	China	PP550880	PP550027	this study
D. naematelioides	YAASM 7490 /-	China	PP550881	_	this study
D. naematelioides	YAASM 7491 /-	China	PP550882	_	this study
D. ovisporus	– /H:Miettinen 20787	Finland	MW191964	MW159074	Savchenko et al. (2021)
D. ovisporus	- /H:Spirin 11145	Norway	MW191960	MW159073	Savchenko et al. (2021)
D. pinacearum	- /UPS:F-593533	Japan	MN595637	MN595637	Zamora and Ekman (2020)
D. pinacearum	- /UPS:F-593535	Japan	MN595638	MN595638	Zamora and Ekman (2020)
D. puniceus	TUFC12833 /TNS-F-15711	Japan	AB712449	AB299057	Shirouzu et al. (2013)
•		•			, ,
D. puniceus	- /Wu180	China	OL587812	OL546780	unpublished
). sinostenosporus	− /Dai 20003 [⊤]	China	MW540888	MW540890	Lian et al. (2022)
). sinostenosporus	- /Dai 20008	China	MW540889	MW540891	Lian et al. (2022)
D. sobrius	CFMR:RLG-13487 [⊤] /-	USA	AB712445	AB712425	Shirouzu et al. (2013)

Species	Isolate ID /Voucher	Country	GenBank Accession Numbers		Deference
			ITS	LSU	Reference
D. stenosporus	ICMP 20488 /PDD 105018 [™]	New Zealand	LC131433	LC131396	Shirouzu et al. (2017)
D. stenosporus	ICMP 21237 /PDD 107970	New Zealand	LC131434	LC131397	Shirouzu et al. (2017)
D. stillatus (anamorph)	- /UPS:F-939814	Sweden	MN595676	MN595676	Zamora and Ekman (2020)
D. stillatus (anamorph)	- /UPS:F-939816	Sweden	-	MN593494	Savchenko et al. (2021)
D. stillatus (teleomorph)	- /UPS:F-939814	Sweden	MN595677	MN595677	Zamora and Ekman (2020)
D. stillatus (teleomorph)	- /UPS:F-939816	Sweden	-	MN593495	Savchenko et al. (2021)
D. subalpinus	TUFC12834 /TNS-F-15730	Japan	AB712465	AB299060	Shirouzu et al. (2013)
D. venustus	− /0:Adane 150 [⊤]	Ethiopia	MW191949	MW159075	Savchenko et al. (2021)
Dacryonaema macnabbii	- /UPS:F-940949	Sweden	MN595650	MN595650	Zamora and Ekman (2020)
D. macnabbii	- /UPS:F-940992	Sweden	MN595653	MN595653	Zamora and Ekman (2020)
D. macrosporum	- /UPS:F-940998	Finland	MN595660	MN595660	Zamora and Ekman (2020)
D. macrosporum	- /UPS:F-941001	Finland	MN595661	MN595661	Zamora and Ekman (2020)
D. rufum	- /UPS:F-941005	Sweden	MN595646	MN595646	Zamora and Ekman (2020)
D. rufum	- /UPS:F-941012	Finland	MN595649	MN595649	Zamora and Ekman (2020)
Dacryopinax elegans	- /TENN 066927	USA	MN595640	MN595640	Zamora and Ekman (2020)
Dacryopinax sp.	- /H7008759	Kenya	MW191959	MW159091	Savchenko et al. (2021)
D. spathularia	TUFC12846 /TNS-F-21048	Japan	AB712473	AB472710	Shirouzu et al. (2013)
D. spathularia	FCME 27539 /-	Mexico	MN733711	MN733722	Castro-Santiuste et al. (202
D. spathularia	- /H:Miettinen 20559	Indonesia	MW191976	MW159092	Savchenko et al. (2021)
Dendrodacrys ciprense	− /UPS:F-946590 [⊤]	Cyprus	OM519385	OM519385	Zamora et al. (2022)
D. ciprense	- /UPS:F-946591	Cyprus	OM519386	OM519386	Zamora et al. (2022)
D. concrescens	− /UPS:F-946602 [™]	Sweden	OM519390	OM519390	Zamora et al. (2022)
D. ellipsosporum	− /UPS:F-946604 [™]	Spain	OM519392	OM519392	Zamora et al. (2022)
D. oblongisporum	− /UPS:F-979568 [⊤]	Spain	OM519400	OM519400	Zamora et al. (2022)
Ditiola peziziformis	- /H:Haikonen 24269	Finland	MW191972	MW159070	Savchenko et al. (2021)
D. peziziformis	- /H:Haikonen 30097	Finland	MN595642	MN595642	Zamora and Ekman (2020)
D. radicata	- /H:Miettinen 20590.2	Finland	MW191966	MW159083	Savchenko et al. (2021)
D. radicata	- /UPS:F-939957	Sweden	MN595641	MN595641	Zamora and Ekman (2020)
Guepiniopsis buccina	- /CWU(MYC)7014	Ukraine	MW191971	MW159086	Savchenko et al. (2021)
G. buccina	- /UPS:F-940947	Spain	MN595643	MN595643	Zamora and Ekman (2020
Unilacryma unispora	- /UPS:F-941279	Sweden	MN595667	MN595667	Zamora and Ekman (2020
U. bispora	- /UPS:F-941254	Sweden	MN595670	MN595670	Zamora and Ekman (2020
U. bispora	- /UPS:F-941266	Sweden	MN595674	MN595674	Zamora and Ekman (2020)
Dacrymycetes sp.	NBRC 110592 /-	Japan	LC004003	LC003884	Shirouzu et al. (2016)
Coprinus comatus	AFTOL-ID 626 /-	USA	AY854066	AY635772	Shirouzu et al. (2013)
Suillus pictus	AFTOL-ID 717 /-	USA	AY854069	AY684154	Shirouzu et al. (2013)

ML and BI analyses generated similar topologies, so only the ML tree is presented along with the support values from the Maximum likelihood bootstrap (BS, >75%) values and Bayesian inference (BI) posterior probabilities (PP, >0.95) (Fig. 1). The phylogeny revealed that Cyphellaceae was divided into three clades, and these three genera of *Incrustocalyptella* Agerer, *Cyphella* Fr., and *Campanophyllum* constituted one of the three major clades with strong statistical supports (99% BS, 1.00 PP). In the ML tree, the phylogenetic results demonstrated that *Campanophyllum microsporum* formed a distinct lineage closely related to *C. proboscideum* and *Campanophyllum* sp. (Voucher NEHU.MBSRJ. 38) with strong statistical supports (98% BS, 0.99 PP). The ITS sequences from *C. microsporum* and *C. proboscideum* were markedly different, with ca. 105 different nucleobases, and the ITS sequences of *C. microsporum* and *Campanophyllum* sp. (Voucher NEHU.MBSRJ. 38) were different with about 20 different nucleobases.

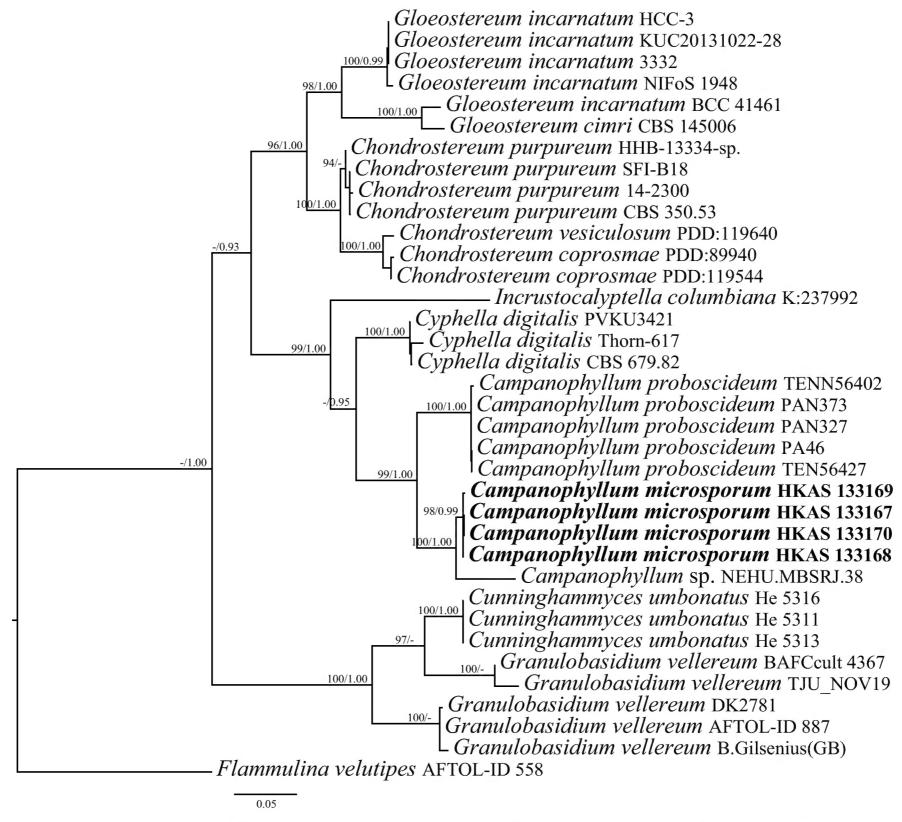


Figure 1. Maximum likelihood (ML) tree of Cyphellaceae based on the combined ITS+LSU dataset. ML bootstrap values (BS > 75%) and Bayesian posterior probabilities (PP > 0.95) are shown at the nodes in the order of BS/PP. The tree is rooted with *Flammulina velutipes*. The new taxon is indicated in bold.

In the phylogeny of Dacrymycetaceae, the concatenated dataset of LSU and ITS sequences comprised a total of 1649 characters. 94 sequences were used for phylogenetic analyses, of which nine sequences were newly generated in this study. ML and BI analyses generated similar topologies, so only the ML tree is presented (Fig. 2). Within Dacrymycetes, we distinguish four main groups, Dacrymycetaceae (clade A), Cerinomycetaceae (clade B), Dacryonaemataceae (clade C), and Unilacrymaceae (clade D). The clade A included several genera and the majority of species, and formed a sister group to the clades B, C, and D with strong statistical support (95% BS, 1.00 PP). Samples of the two new species were placed in the clade A, and one of the new species of Dacrymyces naematelioides formed a non-monophyletic, strongly supported group. The new species Calocera multiramosa was found to be closely related to C. tibetica with high supports (85% BS, 1.00 PP), and the two species clustered together with C. viscosa with strong supports (91% BS, 1.00 PP). The new species D. naematelioides formed a sister lineage to D. chrysospermus with 78% bootstrap support and 1.00 posterior probability.

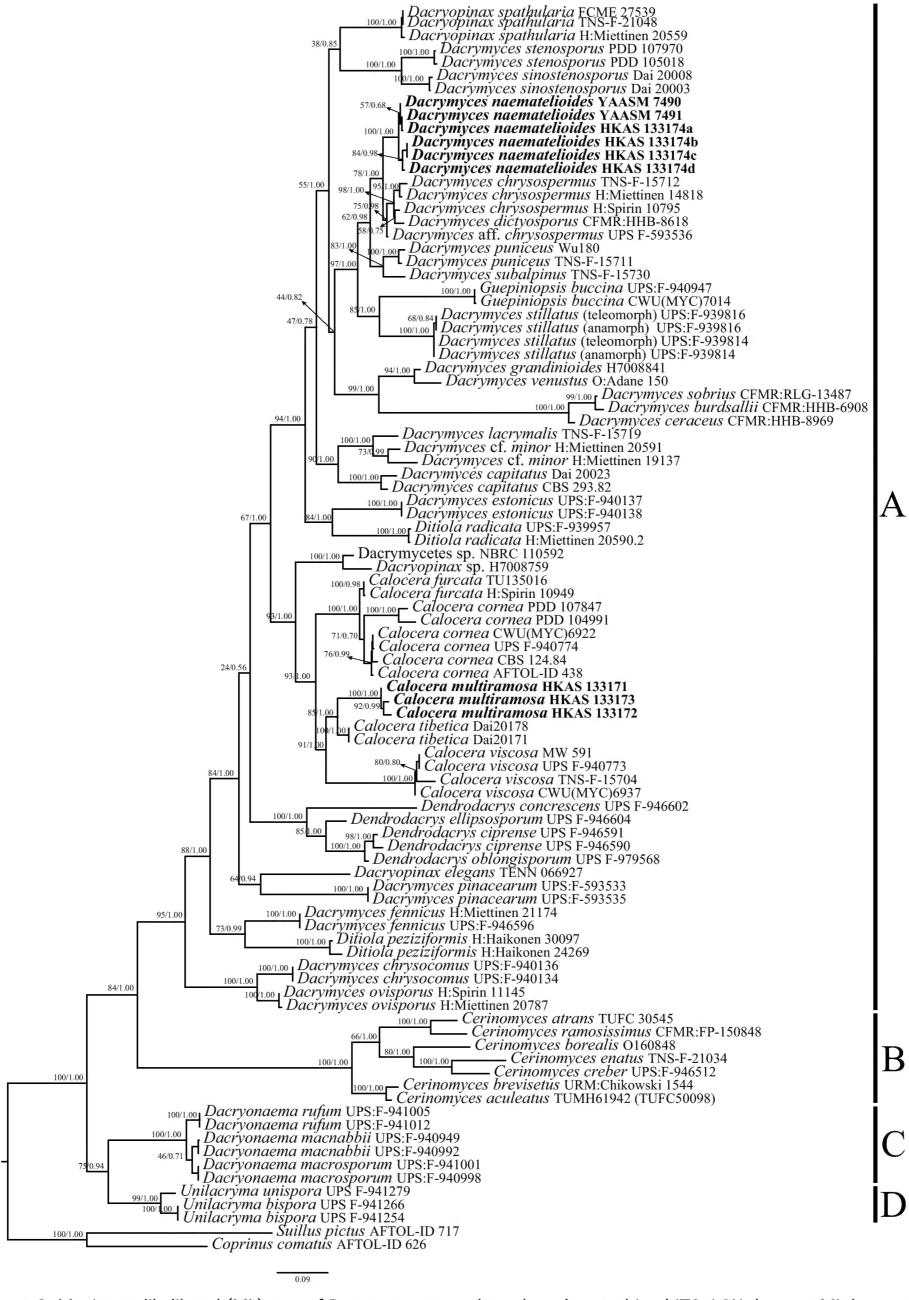


Figure 2. Maximum likelihood (ML) tree of Dacrymycetaceae based on the combined ITS+LSU dataset. ML bootstrap values and Bayesian posterior probabilities are shown at the nodes in the order of BS/PP. The tree is rooted with *Suillus pictus* and *Coprinus comatus*. The new taxon is indicated in bold.

Taxonomy

Campanophyllum microsporum Y.H. Ma, W.M. Chen & Y.C. Zhao, sp. nov.

MycoBank No: 853503

Figs 3-5

Diagnosis. Campanophyllum microsporum is characterized by dorsally pseudostipitate pileus, excentric to lateral pseudostipe, crowded lamellae, cylindrical-ellipsoid basidiospores $(3.0-4.2 \times 1.7-2.2 \mu m)$, narrowly clavate to clavate basidia $(14.5-23.0 \times 3.0-4.0 \mu m)$, and cylindrical to clavate cheilocystidia $(22.0-55.0 \times 5.0-11.0 \mu m)$; occurrence in a deciduous forest and solitary, cespitose, scattered, or gregarious habit on rotten wood.

Type. CHINA. Yunnan Province: Jianchuan County, Laojunshan Town (26°35.85'N, 99°40.44'E, elev. 3100 m), on rotten wood, 21 September 2023, Yuan-Hao Ma, Min Zeng & Wei-Min Chen (Holotype: HKAS 133170!, ex-type: YAASM 7187).

Etymology. The epithet "microsporum" refers to the smaller basidiospores compared to *Campanophyllum proboscideum*.

Description. Basidiomata pseudostipitate, dorsally and eccentrically or laterally attached to substrate, occasionally central, pendent, broadly cyphelloid to crepidotoid, lamellate. Pileus $5.0-12.0\times4.0-9.0$ cm, spathulate, flabelliform to rounded-flabelliform, sometimes subcircular; plano-convex when young and applanate when older, margin inrolled, lobate when fully expanded; surface moist, initially pale orange (5A2-4), greyish orange (5B2-3), or light orange (6A2-5), then brownish orange (6C5-6), light brown (6D5-8), often with small stains of darker colors. Context thick, fleshy, whitish, and unchanging in color when injured. Lamellae extending radially from attachment point within pseudostipe, very crowded, sometimes forked, white to off-white, sometimes with small blackish stains. Pseudostipe $0.5-2.5\times0.4-1.0$ cm, concolorous with pileus, discolouring to blackish-ochre (6E5-7, 6F7). Spore print white. Taste mild, odor indistinct.

Basidiospores [149/7/4] (2.7–)3.0–4.2(–4.5) × (1.5–)1.7–2.2(–2.6) µm, L_m = 3.5 µm, W_m = 1.9 µm, Q = 1.4–2.5, Q_m = 1.8, cylindrical-ellipsoid, smooth, hyaline, thin-walled, inamyloid. Basidia (13.5–)14.5–23.0(–26.0) × (2.3–)3.0–4.2(–4.6) µm, L_m = 17.6 µm, W_m = 3.6 µm, Q = 3.6–7.4, Q_m = 4.9, narrowly clavate to clavate, 4-spored, sterigma 0.9-2.2 µm. Cheilocystidia abundant, (17.5–)22.0–55.0(–59.0) × (4.2–)5.0–10.8(–13.9) µm, L_m = 37.0 µm, W_m = 7.2 µm, hyaline, thin-walled, mostly cylindrical to clavate, sometimes lageniform, rod-like, or beaked-utriform, pedunculate (1.9–12.5 × 1.8–4.1 µm). Pleurocystidia not observed. Lamellar trama hyaline, parallel, hyphae 3.6–17.6 µm in diameter, thin- to thick-walled. Pileipellis composed of repent, parallel hyphae, 4.2–11.5 (–17.0) µm in diameter, sometimes with yellow-brown, intracellular pigments. Clamp connections present in all tissues of basidiomata.

Culture characteristics. Colonies grown on YPD reaching 40 mm radius within 20 days at 22 °C in the dark, forming abundant aerial mycelium, usually zonate. Mycelium irregularly cottony, with common clamp connections, pallid mouse gray to pale brown in aerial mycelium with age, easily forming basidiomata in the Petri plate.

Habitat and distribution. Solitary, cespitose, scattered, or gregarious on rotten wood in a deciduous forest; known from Yunnan, China.

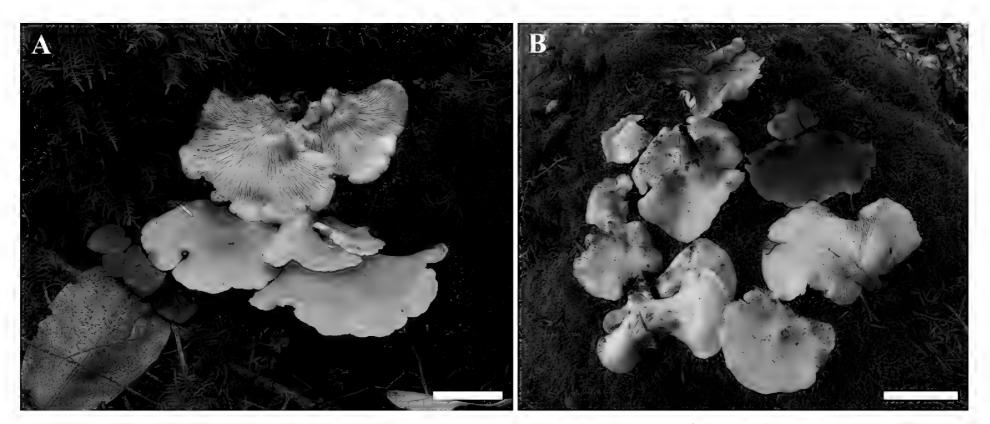


Figure 3. Basidiomata of *Campanophyllum microsporum* in the field **A** HKAS 133170 (Holotype) **B** HKAS 133169. Photos by Y.H. Ma. Scale bars: 3 cm.

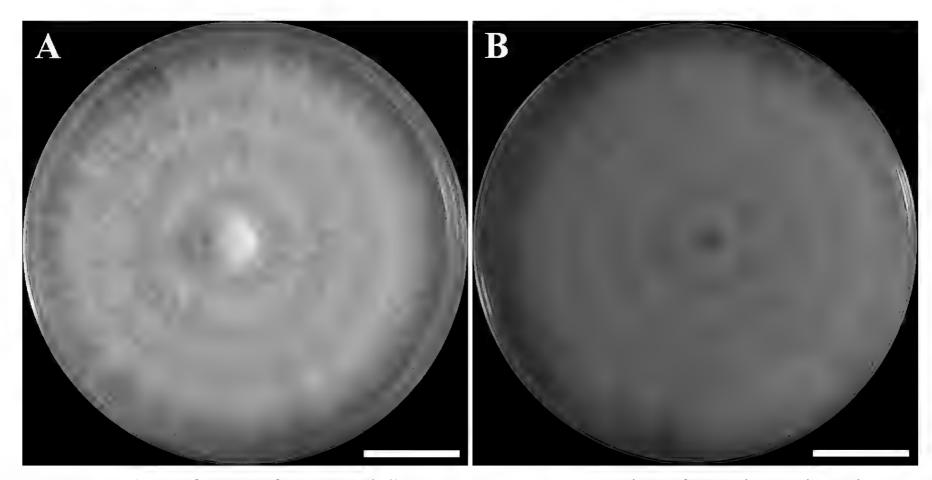


Figure 4. Morphological features of *Campanophyllum microsporum* on YPD medium after 20 days in the dark in a 9 cm Petri plate (ex-type YAASM 7187) **A** surface of colony **B** reverse of colony. Photos by Y.H. Ma. Scale bars: 2 cm.

Additional specimens examined. CHINA, Yunnan Province: Jianchuan County, Laojunshan Town, 7 July 2022, Yuan-Hao Ma, Ping Liu & Yong-Chang Zhao (HKAS 133167, HKAS 133168); 26 July 2023, Yuan-Hao Ma & Ping Liu (HKAS 133169).

Notes. Campanophyllum microsporum is similar to *C. proboscideum* in both macro- and micro-morphology, including broadly cyphelloid to crepidotoid basidiomata, spathulate, flabelliform to rounded-flabelliform pileus, and very crowded lamellae; cylindrical-ellipsoid basidiospores, narrowly clavate to clavate basidia. However, several other features can distinguish the two species. Morphologically, the new species have smaller basidiospores $(3.0-4.2 \times 1.7-2.2 \ \mu m vs. 4-4.5 \times 2-3 \ \mu m)$, slenderer and longer basidia $(14.5-23.0 \times 3.0-4.2 \ \mu m vs. 14-17 \times 4.5-5.0 \ \mu m)$, and larger cheilocystidia $(22.0-55.0 \times 5.0-10.8 \ \mu m vs. 18-25 \times 9-11 \ \mu m)$ (Cifuentes et al. 2003).

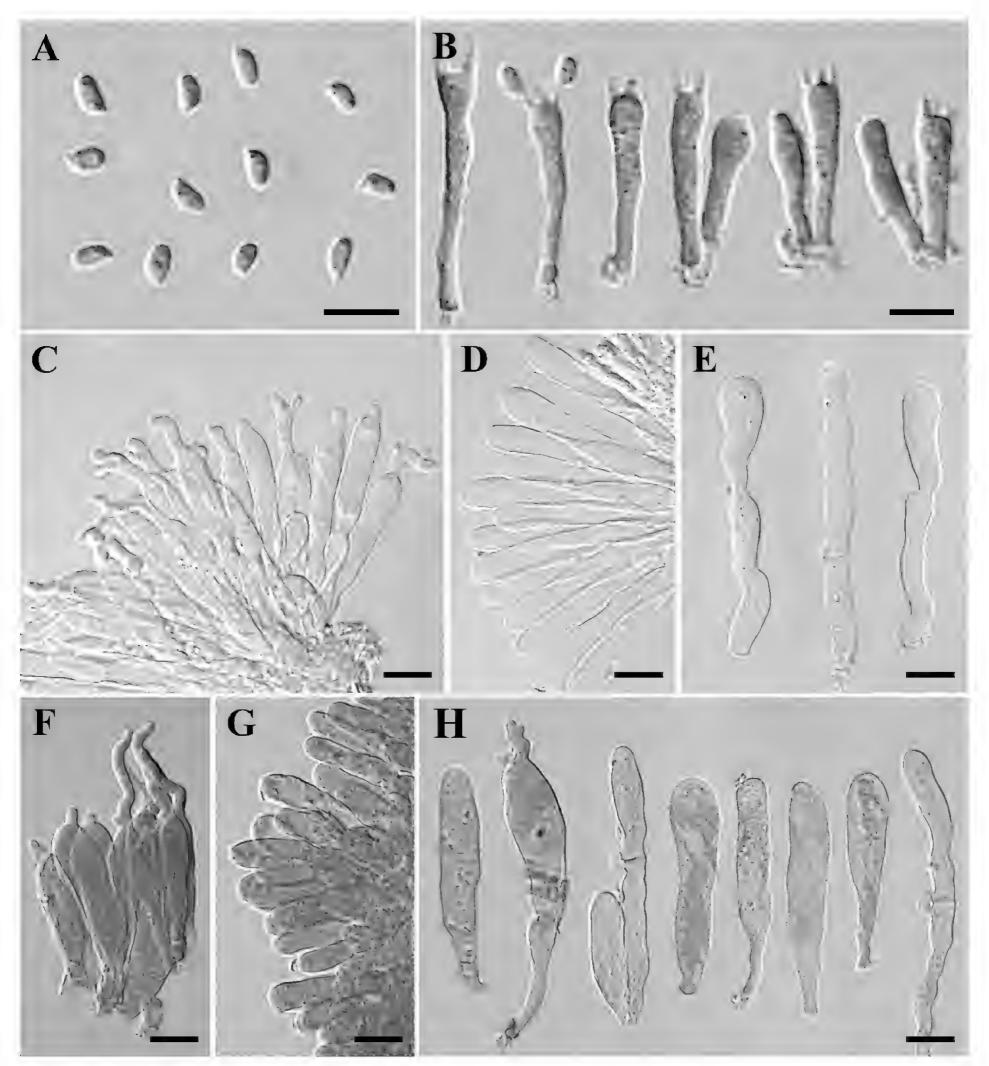


Figure 5. Microscopic structures of *Campanophyllum microsporum* (Holotype HKAS 133170) **A** basidiospores in Congo red **B** basidia in Congo red **C-H** cheilocystidia (**C-E** in KOH solution **F-H** in Congo red). Photos by Y.H. Ma. Scale bars: 10 μm.

Calocera multiramosa Y.H. Ma, W.M. Chen & Y.C. Zhao, sp. nov.

MycoBank No: 853504

Figs 6-8

Diagnosis. Calocera multiramosa differs from other species of the genus by yellowish to orange basidiomata, dendroid and dichotomously branches, branched, smooth, thin-walled marginal hyphae $(2.0-4.8 \mu m)$, branched, thin-

walled internal hyphae (2.9–10.0 μ m), cylindrical to clavate basidia (36.5–52.5 \times 4.0–6.0 μ m), 1–5-septate, navicular or reniform basidiospores (10.4–16.7 \times 5.2–7.4 μ m), occurrence in a deciduous or coniferous forest, occasionally scattered habit on standing timber.

Type. CHINA. Yunnan Province: Shangri-La County, Pudacuo National Park (27°50.61'N, 99°57.03'E, elev. 3800 m), on standing timber, 17 August 2020, Yuan-Hao Ma, Hong-Mei Chai & Wei-Min Chen (Holotype: HKAS 133171!).

Etymology. The epithet "multiramosa" refers to abundant branches of basidiomata.

Description. Basidiomata stipitate, fasciculate, usually geminate, occasionally scattered, gelatinous, 1.5–4.0 cm in height, tough, dendroid and dichotomously branched, cylindrical or flattened, surface smooth, yellowish to orange (5B8, 6A8, 6B7–8), 0.3–0.5 cm in diameter at the upper branching part. Marginal hyphae on sterile surfaces cylindrical, branched, smooth, straight or flexuous, septate, thin-walled, hyaline, 2.0–4.8 μm in diameter. Internal hyphae branched, septate, thin-walled, hyaline, 2.9–10.0 μm in diameter. Hymenium limited to the upper surface of basidomata, amphigenous, composed of basidia and simple cylindrical hyphidia; hyphidia hyaline or pale yellow, smooth, thin-walled. Subhymenial hyphae hyaline, smooth or scabrous, thin- or slightly thick-walled, 2.5–7.3 μm in diameter. Basidia cylindrical to clavate, hyaline or pale yellow, thin-walled,

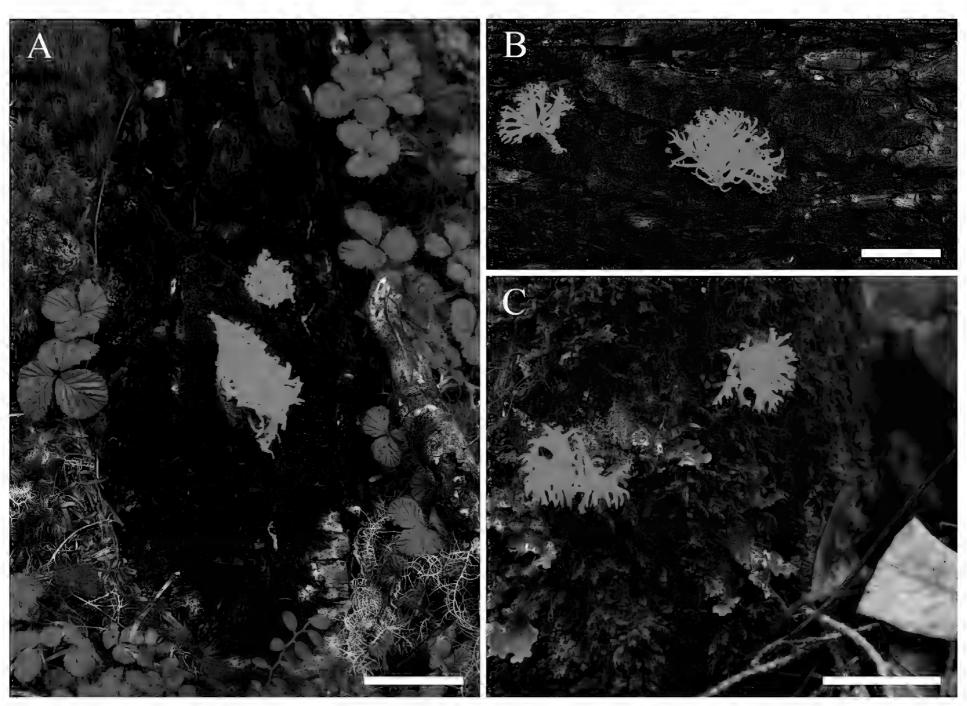


Figure 6. Basidiomata of *Calocera multiramosa* **A** HKAS 133171 (Holotype) **B** HKAS 133172 **C** HKAS 133173. Photos by Y.H. Ma. Scale bars: 3 cm.

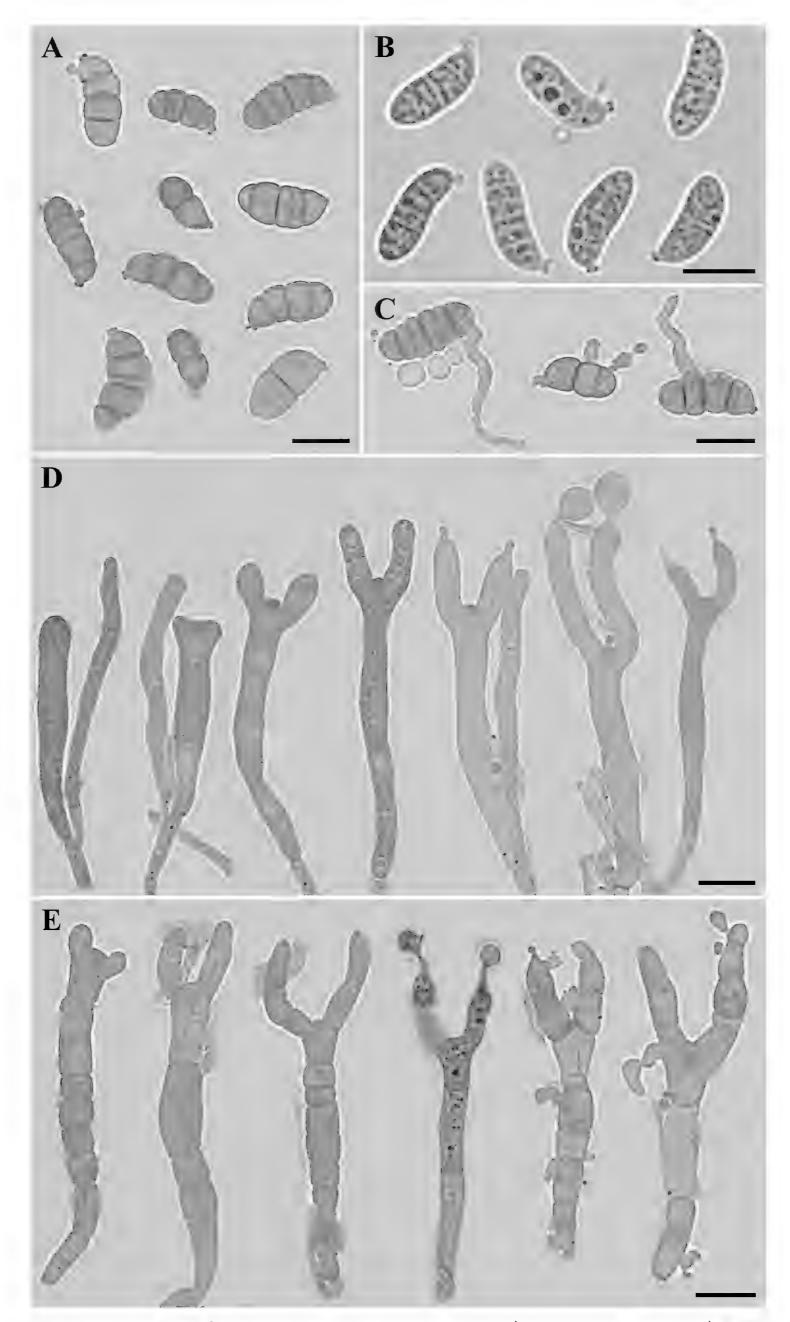


Figure 7. Microscopic structures of *Calocera multiramosa* in Congo red (Holotype HKAS 133171) **A**, **B** basidiospores **C** germinating basidiospores **D** probasidia, developing basidia and hyphidia **E** abnormal developing basidia with septa and geminations. Photos by Y.H. Ma. Scale bars: $10 \, \mu m$.

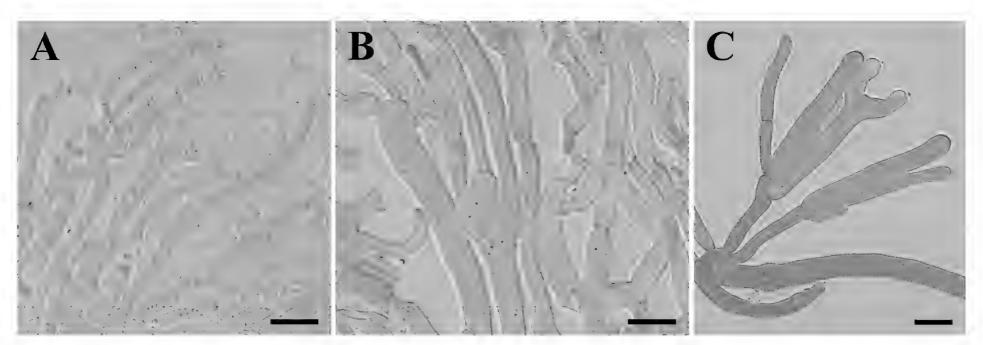


Figure 8. Microscopic structures of *Calocera multiramosa* in Congo red (Holotype HKAS 133171) **A** marginal hyphae **B** internal hyphae **C** subhymenial hyphae, probasidia, developing basidia, and hyphidia. Photos by Y.H. Ma. Scale bars: 10 μm.

becoming bifurcate when mature, $(33.5-)36.5-52.5(-55.0) \times (3.5-)3.8-6.1(-6.4)$ µm, $L_m = 45.1$ µm, $W_m = 4.9$ µm, sometimes with many septa. Basidiospores [102/3/3], navicular or reniform, straight or curved, with a small apiculum at the top, thin-walled with thin septa, hyaline to pale yellow, sometimes with oil drops when young and in the germination stage, $(6.5-)10.4-16.7(-17.0) \times (4.5-)5.2-7.4(-8.8)$ µm, $L_m = 14.3$ µm, $W_m = 6.3$ µm, Q = (1.4-)1.6-2.7(-2.8), $Q_m = 2.3$, 1-5-septate at maturity. Germination with conidia by abnormally developing basidia with lots of septa, by hyphae with septa, or by germ tubes. Clamp connections absent in all tissues of the basidiomata.

Habitat and distribution. Geminate, occasionally scattered on standing timber in a deciduous or coniferous forest; known from Yunnan, China.

Additional specimens examined. CHINA. Yunnan Province: Shangri-La County, Pudacuo National Park, 28 August 2021, Yuan-Hao Ma, Ping Liu & Yong-Chang Zhao (HKAS 133172); Jianchuan County, Laojunshan Town, 26 July 2023, Yuan-Hao Ma & Ping Liu (HKAS 133173).

Notes. Calocera multiramosa resembles C. tibetica, C. viscosa and C. mangshanensis in dendrite basidiomata. However, C. multiramosa is distinguished from C. tibetica by larger basidiospores (10.4–16.7 \times 5.2–7.4 μ m vs. 9.0–13.0 \times 5.0-6.0 µm) with different septa (1-5 vs. 3-4) (Fan et al. 2021); C. multiramosa differs from C. viscosa in larger basidia (36.5-52.5 × 3.8-6.1 μm vs. $23-42 \times 3-4.5 \mu m$) and basidiospores with different septa (1-5 vs. 0-1) (McNabb 1965; Shirouzu et al. 2009). C. multiramosa can be distinguished from C. mangshanensis by larger (10.4–16.7 \times 5.2–7.4 μ m vs. 10.0–13.0 \times $4.5-5.5 \mu m$), more septate (1-5 vs. 0-1) basidiospores (Liu and Fan 1989). The new species grows on angiosperm and gymnosperm wood, while C. tibetica and C. viscosa only grows on gymnosperm wood and C. mangshanensis only grows on decayed angiosperm wood (McNabb 1965; Liu and Fan 1989; Oberwinkler 2014). C. multiramosa can be distinguished from C. cornea by the size of the basidiomata (1.5-4.0 cm vs. 0.1-0.5 cm high) (Shirouzu et al. 2009), and C. furcata by the mature basidiospores with different septa (1-5 vs. 1-3) (McNabb 1965). The specimen of C. multiramosa, collected from the Laojun Mountain could not be designated as the holotype because of many immature basidiospores. Therefore, the specimen of C. multiramosa collected from a coniferous forest in the Pudacuo National Park was designated as the holotype.

Dacrymyces naematelioides Y.H. Ma, W.M. Chen & Y.C. Zhao, sp. nov.

MycoBank No: 853505

Figs 9-11

Diagnosis. Dacrymyces naematelioides differs from other species of the genus by stipitate and cerebriform basidiomata, smooth or roughened, simple or branched, septate marginal hyphae $(3.0-8.5~\mu m)$, smooth or roughened, thin-walled, branched, and septate internal hyphae $(2.3-11.0~\mu m)$, cylindrical to clavate, smooth or roughened basidia $(38.5-79.5\times6.5-10.6~\mu m)$, broadly elliptic-fusiform, 7-septate mature basidiospores $(18.5-28.6\times8.9-13.8~\mu m)$, the absence of clamp connections, occurrence in a deciduous forest, and fasciculate, gregarious, or scattered habit on rotten wood.

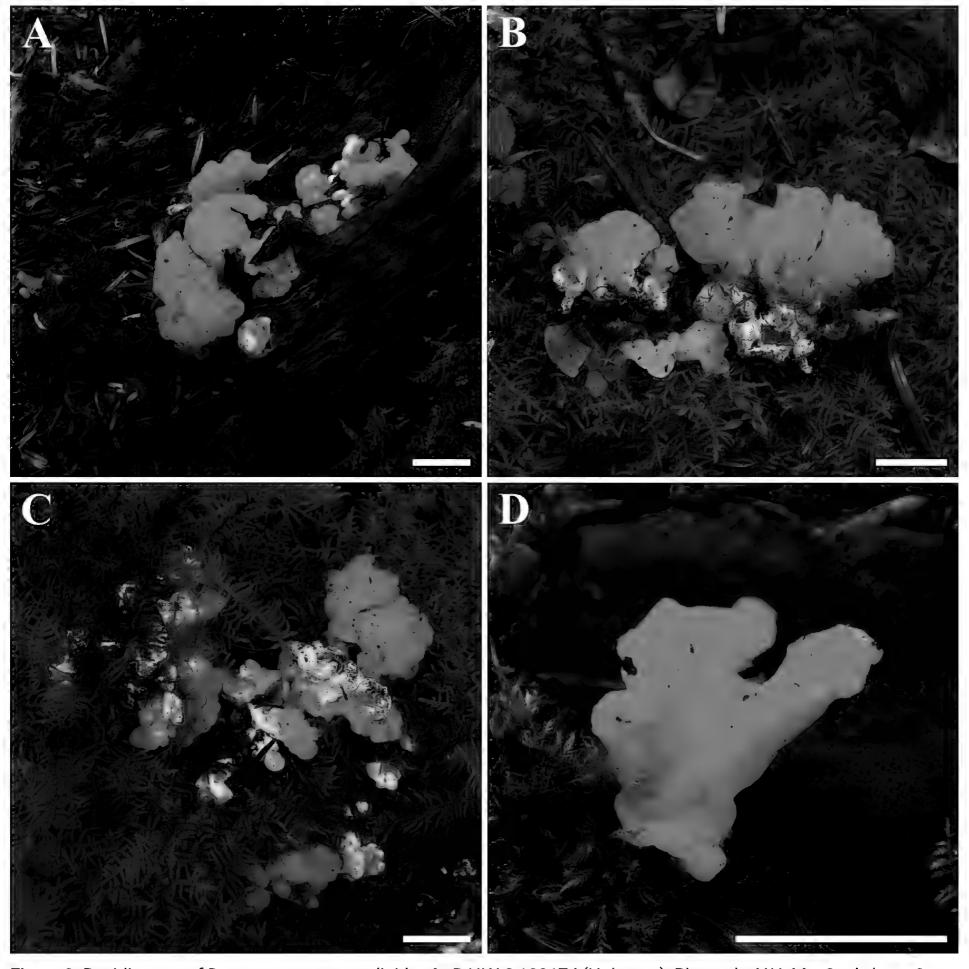


Figure 9. Basidiomata of *Dacrymyces naematelioides* A-D HKAS 133174 (Holotype). Photos by Y.H. Ma. Scale bars: 3 cm.

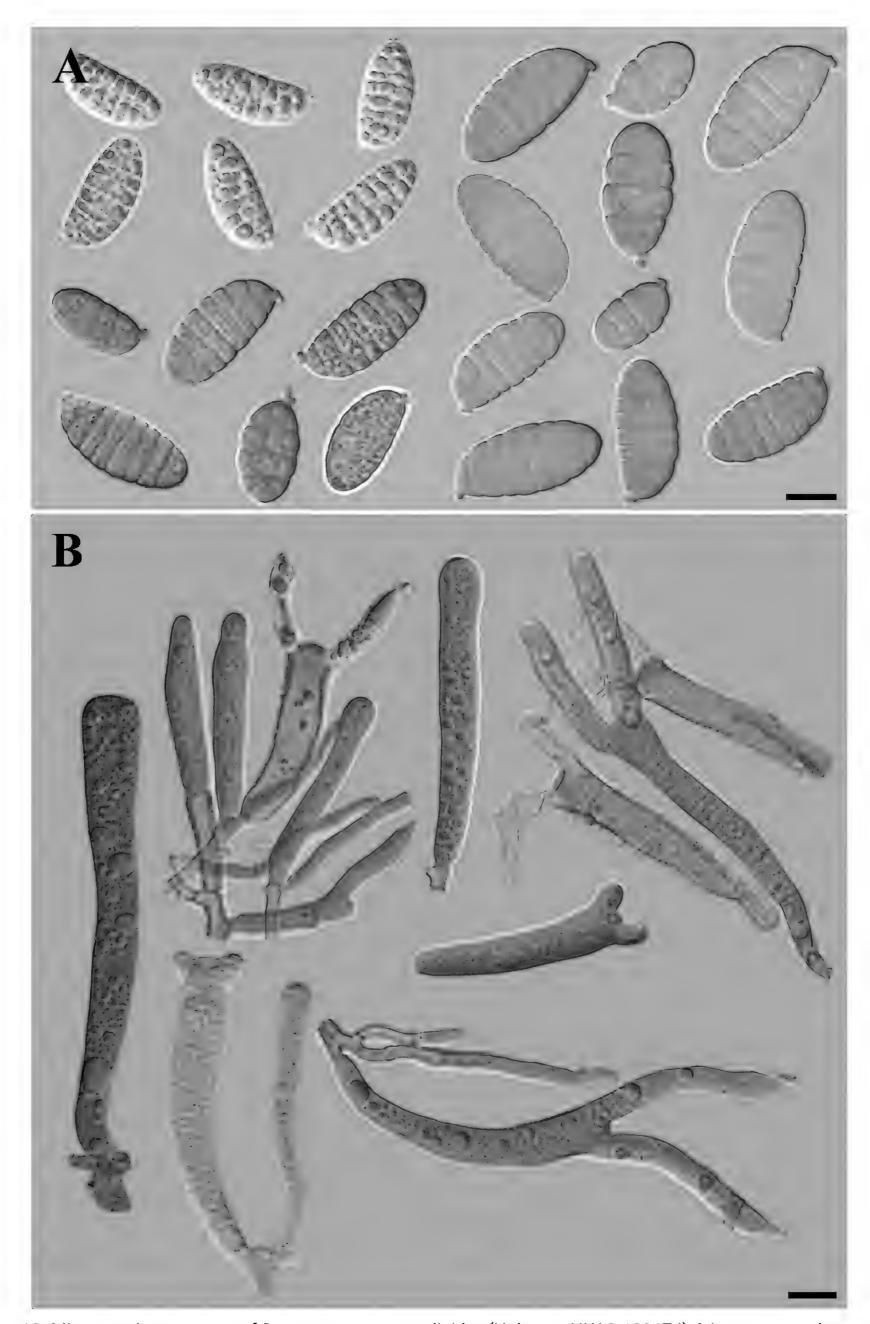


Figure 10. Microscopic structures of *Dacrymyces naematelioides* (Holotype HKAS 133174) $\bf A$ immature and mature basidiospores in Congo red and KOH solution $\bf B$ probasidia, developing basidia and hyphidia in Congo red. Photos by Y.H. Ma. Scale bars: 10 μ m.



Figure 11. Microscopic structures of *Dacrymyces naematelioides* (Holotype HKAS 133174) **A** marginal hyphae **B** internal hyphae **C** subhymenial hyphae. Photos by Y.H. Ma. Scale bars: 10 μm.

Type. CHINA. Yunnan Province: Jianchuan County, Laojunshan Town (26°35.86'N, 99°40.46'E, elev. 3100 m), 21 September 2023, Yuan-Hao Ma, Min Zeng & Wei-min Chen (Holotype: HKAS 133174!).

Etymology. The epithet "naematelioides" refers to the similarity of the new species in terms of macromorphological features to *Naematelia aurantialba*.

Description. Basidiomata stipitate, fasciculate and conspicuous, gregarious or scattered, gelatinous when fresh, cerebriform, 2.5-4.5 cm high, surface smooth, orange to light brown (6A8, 6D7-8), occasionally colorless, stipe flat cylindrical, usually with white hairs. Marginal hyphae on sterile surfaces of basidiocarps cylindrical, simple or branched, smooth or roughened, straight or flexuous, septate, thick-walled, hyaline, 3.0-8.5 µm in diameter. Internal hyphae branched, septate, thin-walled, hyaline, smooth or roughened, 2.3-11.0 µm in diameter. Hymenium limited to the upper surface of the basidoma, amphigenous, composed of basidia and simple cylindrical hyphidia; hyphidia hyaline or pale yellow, smooth, thin-walled. Subhymenial hyphae, smooth or roughened, thin- to thick-walled, 2.5-5.3 µm in diameter. Basidia cylindrical to clavate, smooth or roughened, pale yellow, thin-walled, becoming bifurcate, $(30.0-)38.5-79.5(-83.5) \times (5.5-)6.5-10.6(-11.1) \mu m$, $L_m = 60.2 \mu m$, W_m = 8.3 μm. Basidiospores [95/5/1], broadly and elliptic-fusiform, with a small apiculum at the base, thin-walled, pale yellow, with oil drops when young, $(16.5-)18.5-28.5(-29.5) \times (8.7-)8.9-13.8(-14.6) \mu m$, $L_m = 23.9 \mu m$, $W_m = 11.0$ μ m, Q = (1.5–)1.8–2.4(–2.5), Q $_{\rm m}$ = 2.2, usually 7–septate, rarely 3– or 4– septate at maturity. Germination not observed. Clamp connections absent in all tissues of the basidiomata.

Habitat and distribution. Fasciculate, gregarious, or scattered habit on rotten wood, and occurrence in a deciduous forest; known from Yunnan, China.

Notes. Dacrymyces naematelioides resembles D. chrysospermus and D. dictyosporus in shape and size of basidiomata. Microscopically, D. chrysospermus differs from D. naematelioides by narrower basidia (4–6.5 μ m vs. 6.5–10.6 μ m in width) and smaller basidiospores (16.5–23 × 5–7.5 μ m vs. 18.5–28.6 ×8.9–13.8 μ m), and D. dictyosporus differs by smooth basidia and thick-walled basidiospores (Martin et al. 1958; McNabb 1973).

Discussion

In this study, we described three new species from Yunnan Province, China, based on morphological evidence and multi-locus phylogenic analyses. The identified morphological features of *Campanophyllum* include dorsally pseudostipitate pileus, excentric to lateral pseudostipe, and crowded lamellae (Cifuentes et al. 2003; Reschke et al. 2021). The specimen of *Campanophyllum* sp. (Voucher NEHU.MBSRJ. 38) reported from India formed a sister lineage to *C. microsporum* with strong supports (100% BS, 1.00 PP). The specimen (Voucher NEHU.MBSRJ. 38) is presumably a new species in the genus *Campanophyllum* based on the phylogenetic trees (Fig. 1), but it needs to be further confirmed. Meanwhile, our research indicates that more new species of this genus will be discovered in China. However, their habitat is in decline and disappearing.

The species of *Calocera* in the family Dacrymycetaceae are typically distinguished morphologically based on simple or forked clavarioid basidiocarps (Oberwinkler 2014), but the genus *Dacrymyces* includes more than 30 species with variable basidiomata including pulvinate, discoid, turbinate, spathulate, flabellate, and cylindrical forms (McNabb 1973; Shirouzu et al. 2009). Several species of *Dacrymyces* are morphologically close to *Calocera* by sharing spathulate or cylindrical basidioma, and yet they can be distinguished by some other morphological features, such as the septa of the basidiospores, morphology of the basidia, and morphology of the marginal hyphae. More appropriate genus boundaries and definitions can be obtained by studying detailed morphological and molecular data on more specimens of Dacrymycetaceae. Continuing collection efforts and herbarium searches in unidentified Dacrymycetaceae will certainly uncover more new species (Savchenko et al. 2021).

Phylogenetic analyses, based on two combined loci (ITS, LSU), as well as morphological characteristics, are important for the identification of *Calocera* and *Dacrymyces* species. The two newly proposed species formed separate branches on the phylogenetic trees with strong statistical support, and the phylogenies for the genera presented here were found to be similar to those of previous studies (Shirouzu et al. 2013). The results of our study indicated that the specimens of *Dacrymyces naematelioides* collected from the same locality formed two distinct clades in the phylogenetic analysis (Fig. 2) with strong statistical support (100% BS, 1.00 PP), but there is no marked difference in their morphological characteristics. This suggests that there may be some variation in this species at the molecular level.

The abnormal developing basidia and probasidia with a lot of septa in specimens of *Calocera multiramosa* were also observed clearly under the microscope, and sometimes they can germinate with microconidia in the basidiomata. This microscopic feature may also be useful in identifying species in the genus *Calocera*. The surface of the basidia of the *Dacrymyces naematelioides* is smooth or roughened (Fig. 9). However, the surface features of the basidia did not seem to have been noted in much of the literature, and it is likely that in most species the surface of the basidia is smooth or has only one morphological feature.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

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Data availability

All of the data that support the findings of this study are available in the main text.

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